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BOTANY.—*Realignments in the Bromeliaceae subfamily Tillandsioideae.* LYMAN B. SMITH, Department of Botany, U. S. National Museum, and COLIN S. PITTENDRIGH,[1] Department of Biology, Princeton University.

It has long been evident that no author has been consistent or logical in delimiting the genera of the subfamily Tillandsioideae of the Bromeliaceae. Virtually all useful phylogenetic characters are limited to the petals, stamens, and pistil, yet available material is so frequently inadequate in these parts, that there is a tremendous temptation to base genera on other characters. The assumption has been that certain habital characters are correlated with floral ones. This is true in a single instance, the absence of spines on the leaves of the Tillandsioideae. All other correlations in the subfamily are incomplete to begin with as in the case of the distichous arrangement of flowers that partially characterizes *Tillandsia* and *Vriesia*, or else they have broken down with the discovery of additional species.

We do not believe in making changes on well established systems such as the latest monograph of the family (Mez in Engler, Das Pflanzenreich IV. **32**) unless something demonstrably better can be offered, but the three genera noted below, *Thecophyllum* André, *Cipuropsis* Ule, and *Chirripoa* Suesseng., are now useless even in an artificial system. Although the generic position of many species must remain in doubt until good flowers are obtained, we are transferring all species on the basis of such evidence as is available. We preface our treatment of *Thecophyllum* and *Cipuropsis* by a concept of *Vriesia* Lindley emended appropriately to include these entities in the sense used by Mez in his last monograph. *Guzmania* requires no emendation to accommodate *Thecophyllum* in the original sense of André.

Vriesia Lindl. emend. Smith & Pittendrigh

Inflorescentia simplex vel paniculata, ea paniculata cum bracteis primariis vel parvis et inconspicuis vel conspicuis et ramos plus minusve obtegentibus; sepalis liberis; petalis vel in tubum brevem sepalis valde superatum connatis vel omnino liberis, appendiculatis; ovario supero vel paulo infero.

Lindley's type species, *V. psittacina*, is gamopetalous, but this fact has been overlooked and the genus characterized as polypetalous, as will be detailed in another paper. As defined above, *Vriesia* contains all the species of the Tillandsioideae with a primary type of gamopetaly, that is, with petals truly fused or connate and not merely agglutinated and more or less interlocking as in the secondary type that characterizes *Guzmania* and *Mezobromelia*. Since it also contains polypetalous species, its basic character remains its appendaged petals.

Thecophyllum André

(Structure of corolla noted where known)

Theccophyllum André, Bromel. Andr. 107. 1889 = **Guzmania** R. & P. Fl. **3**: 37. 1802, in all probability. Of the two original species, the first, *T. wittmackii*, is undoubtedly a *Guzmania*, while the second, *T. poortmanii*, very likely is also although its corolla is still unknown to us. See below.

Thecophyllum André emend. Mez, Bull. Herb. Boiss. II. **3**: 131. 1903 = **Vriesia** Lindl. Bot. Reg. **29**: *pl. 10*. 1843.

T. acuminatum L. B. Smith, Contr. Gray Herb. **117**: 30, *pl. 2, figs. 28, 29*. 1937 = **Vriesia attenuata** Sm. & Pitt. nom. nov. Not *Vriesia acuminata* Mez & Wercklé, Bull. Herb. Boiss. II. **4**: 868. 1904. Petals appendaged—LBS.

[1] This author acknowledges assistance in the course of his work from the Eugene Higgins Memorial Fund, Princeton University.

T. angustum Mez & Wercklé, Bull. Herb. Boiss. II. **4**: 1121. 1904 = **Guzmania donnellsmithii** Mez ex Donn. Smith, Bot. Gaz. **35**: 9. 1903. Petals naked, agglutinated—LBS.

T. balanophorum (Mez) Mez, Bull. Herb. Boiss. II. **3**: 131. 1903. *Guzmania balanophora* Mez in DC. Monogr. Phan. **9**: 918. 1896 = **Vriesia balanophora** (Mez) Sm. & Pitt. comb. nov. Petals appendaged, free—LBS.

T. balanophorum var. *subpictum* Suesseng. Bot. Jahrb. **72**: 291. 1942. From the description this appears to be the same as *T. lineatum* Mez & Wercklé. See below.

T. bracteosum Mez & Wercklé, Repert. Sp. Nov. Fedde **14**: 246. 1916 = **Vriesia bracteosa** (Mez & Wercklé) Sm. & Pitt. comb. nov. Not *Vriesia bracteosa* Beer, Bromel. 263. 1857, nomen in synonymy.

T. capitatum Mez & Wercklé, Bull. Herb. Boiss. II. **4**: 873. 1904 = **Vriesia capitata** (Mez & Wercklé) Sm. & Pitt. comb. nov.

T. capituligerum (Griseb.) L. B. Smith, Contr. Gray Herb. **98**: 14. 1932. *Tillandsia capituligera* Griseb. Cat. Pl. Cub. 254. 1886 = **Vriesia capituligera** (Griseb.) Sm. & Pitt. comb. nov. Petals connate—CSP.

T. comatum Mez & Wercklé, Bull. Herb. Boiss. II. **4**: 871. 1904 = **Vriesia comata** (Mez & Wercklé) Sm. & Pitt. comb. nov.

T. cornuaultii (André) Mez, Engl. Pflanzenreich IV. **32**: 423. 1935. *Tillandsia cornuaulti* André, Énum. Bromél. 8. Dec. 13, 1888; Rev. Hort. **60**: 568. Dec. 16, 1888 = **Tillandsia turneri** Baker, Journ. Bot. **26**: 144. 1888. See L. B. Smith, Contr. Gray Herb. **104**: 82. 1934. Petals naked, free—André sketch.

T. crassiflorum Mez & Wercklé, Bull. Herb. Boiss. II. **3**: 138. 1903 = **Vriesia crassiflora** (Mez & Wercklé) Sm. & Pitt. comb. nov.

T. cylindraceum Suesseng. & Goeppinger, Bot. Jahrb. **72**: 292. 1942 = **Vriesia cylindracea** (Suesseng. & Goeppinger) Sm. & Pitt. comb. nov. The specific name is uncomfortably close to that of *V. cylindrica* L. B. Smith, Contr. U. S. Nat. Herb. **29**: 445. 1951, but we believe it is enough different to obviate the use of a new name.

T. discolor Mez & Wercklé, Repert. Sp. Nov. Fedde **14**: 246. 1916 = **Vriesia discolor** (Mez & Wercklé) Sm. & Pitt. comb. nov.

T. dussii (Mez) Mez, Bull. Herb. Boiss. II. **3**: 131. 1903 = **Guzmania dussii** Mez in DC. Monogr. Phan. **9**: 923. 1896. See L. B. Smith, Contr. Gray Herb. **98**: 30, *pl. 5*, *figs. 13*, *14*. 1932. Petals naked, agglutinated—LBS.

T. fastuosum (André) Mez, Engl. Pflanzenreich IV. **32**: 423. 1935. *Tillandsia fastuosa* André, Énum. Bromél. 8. Dec. 13, 1888; Rev. Hort. **60**: 568. Dec. 16, 1888 = **Vriesia capituligera** (Griseb.) Sm. & Pitt. See above. Petals connate—CSP.

T. gloriosum (André) Mez, Bull. Herb. Boiss. II. **3**: 131. 1903. *Caraguata gloriosa* André, Énum. Bromél. 5. Dec. 13, 1888; Rev. Hort. **60**: 565. Dec. 16, 1888 = **Guzmania gloriosa** (André) André ex Mez in DC. Monogr. Phan. **9**: 922. 1896. See André, Brom. Andr. 48, *pl. 17C*. 1889, where the corolla is described as "breviter trilobata"; L. B. Smith, Caldasia **3**: 240. 1945. Petals naked, agglutinated—André figure.

T. hygrometricum (André) Mez, Bull. Herb. Boiss. II. **3**: 131. 1903. *Caraguata hygrometrica* André, Énum. Bromél. 6. Dec. 13, 1888; Rev. Hort. **60**: 566. Dec. 16, 1888 = **Vriesia hygrometrica** (André) Sm. & Pitt. comb. nov.

T. insigne (E. Morren) Mez, Bull. Herb. Boiss. II. **3**: 131. 1903. *Pepinia insignis* E. Morren ex Baker, Handb. Bromel. 142. 1889 = **Tillandsia insignis** (E. Morren) Sm. & Pitt. comb. nov. Petals free, naked—LBS.

T. irazuense Mez & Wercklé, Bull. Herb. Boiss. II. **3**: 138. 1903 = **Vriesia irazuensis** (Mez & Wercklé) Sm. & Pitt. comb. nov.

T. johnstonii Mez, Bull. Herb. Boiss. II. **4**: 872. 1904, as *johnstonei* = **Vriesia johnstonii** (Mez) Sm. & Pitt. comb. nov. Petals appendaged, free—CSP.

T. kraenzlinianum (Wittm.) Mez, Bull. Herb. Boiss. II. **3**: 131. 1903 = **Guzmania kraenzliniana** Wittm. Bot. Jahrb. **11**: 62. 1890, where the corolla-tube is noted.

T. kupperi Suesseng. & Goepping. Bot. Jahrb. 72: 292. 1942 = **Vriesia kupperi** (Suesseng. & Goepping.) Sm. & Pitt. comb. nov. According to the International Rules, the above combination is not invalidated by *Vriesia kupperiana* Suesseng. Bot. Archiv Leipzig **39**: 384, *fig. 1*. 1939. Petals originally described as free and appendaged.

T. latissimum Mez & Wercklé, Bull. Herb. Boiss. II. **4**: 1122. 1904 = **Vriesia latissima** (Mez & Wercklé) Sm. & Pitt. comb. nov.

T. laxum Mez & Wercklé, Bull. Herb. Boiss. II. **4**: 1123. 1904 = **Vriesia diffusa** Sm. & Pitt. nom. nov. Not *Vriesia laxa* (Griseb.) Mez in DC. Monogr. Phan. **9**: 578. 1896.

T. lehmannianum Mez, Repert. Sp. Nov. Fedde **16**: 72. 1919 = **Guzmania mosquerae** (Wittm.) Mez in DC. Monogr. Phan. **9**: 924. 1896. See below.

T. lineatum Mez & Wercklé, Bull. Herb. Boiss. II. **4**: 875. 1904 = **Vriesia lineata** (Mez & Wercklé) Sm. & Pitt. comb. nov. Petals appendaged, free—LBS.

T. longipetalum (Baker) Mez, Bull. Herb. Boiss. II. **3**: 131. 1903. *Tillandsia longipetala* Baker, Journ. Bot. **26**: 142. 1888 = **Guzmania longipetala** (Baker) Mez in DC. Monogr. Phan. **9**: 919. 1896. See L. B. Smith, Contr. Gray Herb. **104**: 75. 1934. Petals naked, agglutinated—LBS.

T. montanum L. B. Smith ex Yuncker, Field Mus. Pub. Bot. **17**: 319, *pl. 7*. 1938 = **Vriesia montana** (L. B. Smith) Sm. & Pitt. Journ. Washington Acad. Sci. **43**: 69. 1953.

T. mosquerae (Wittm.) Mez, Bull. Herb. Boiss. II. **3**: 131. 1903. *Caraguata mosquerae* Wittm. Bot. Jahrb. **11**: 58. 1889 = **Guzmania mosquerae** (Wittm.) Mez in DC. Monogr. Phan. **9**: 924. 1896. See L. B. Smith, Caldasia no. **5**: 6. 1942.

Petals naked, agglutinated—LBS. Long corolla-tube noted in original description.

T. ororiense (Mez) Mez, Bull. Herb. Boiss. II. **3**: 131. 1903. *Guzmania ororiensis* Mez in DC. Monogr. Phan. **9**: 917. 1896 = **Vriesia ororiensis** (Mez) Sm. & Pitt. comb. nov. Petals described by Mez as free and appendaged in making the combination and in emending *Thecophyllum*.

T. palustre (Wittm.) Mez, Bull. Herb. Boiss. II. **3**: 131. 1903. *Caraguata palustris* Wittm. Bot. Jahrb. **11**: 58. 1889 = **Guzmania palustris** (Wittm.) Mez in DC. Monogr. Phan. **9**: 923. 1896. Corolla-tube noted in original description.

T. paniculatum Mez & Wercklé, Bull. Herb. Boiss. II. **4**: 1123. 1904, as *panniculatum* = **Vriesia triflora** Sm. & Pitt. nom. nov. Not *Vriesia paniculata* (L.) Mez in DC. Monogr. Phan. **9**: 614. 1896.

T. pauperum Mez & Sodiro, Bull. Herb. Boiss. II. **4**: 876. 1904 = **Vriesia paupera** (Mez & Sodiro) Sm. & Pitt. comb. nov.

T. pedicellatum Mez & Wercklé, Bull. Herb. Boiss. II. **3**: 136. 1903 = **Vriesia pedicellata** (Mez & Wercklé) Sm. & Pitt. comb. nov.

T. pennellii (L. B. Smith) Mez. Engl. Pflanzenreich IV. **32**: 422. 1935 = **Guzmania pennellii** L. B. Smith, Contr. Gray Herb. **98**: 30, *pl. 6, fig. 3*. 1932. Confirmed as a *Guzmania* by a subsequent collection (*Cuatrecasas, Schultes & E. Smith* 12743).

T. pictum Mez & Wercklé, Bull. Herb. Boiss. II. **4**: 874. 1904 = **Vriesia picta** (Mez & Wercklé) Sm. & Pitt. comb. nov. Petals appendaged—Mez.

T. pittieri Mez, Bull. Herb. Boiss. II. **3**: 137. 1903 = **Vriesia notata** Sm. & Pitt. nom. nov. Not *Vriesia pittieri* Mez, Bull. Herb. Boiss. II. **3**: 135. 1903. Petals free, appendaged—Mez.

T. poortmanii André, Brom. Andr. 108. 1889, as *poortmani*; Mez, Bull. Herb. Boiss. II. **3**: 131. 1903 = **Guzmania poortmanii** (André) André ex Mez in DC. Monogr. Phan. **9**: 922. 1896, as *poortmani*. Long corolla-tube noted in original description.

T. rubrum Mez & Wercklé, Bull. Herb. Boiss. II. **4**: 878. 1904 = **Vriesia leptopoda** Sm. & Pitt. nom. nov. Not *Vriesia rubra* (R. & P.) Beer, Bromel. 98. 1857.

T. sceptrum Mez, Bull. Herb. Boiss. II. **3**: 139. 1903 = **Guzmania gloriosa** (André) André ex Mez in DC. Monogr. Phan. **9**: 922. 1896. See L. B. Smith, Caldasia **3**: 240. 1945.

T. singuliflorum Mez & Wercklé, Bull. Herb. Boiss. II. **4**: 870. 1904 = **Vriesia singuliflora** (Mez & Wercklé) Sm. & Pitt. comb. nov.

T. sintenisii (Baker) Mez, Bull. Herb. Boiss. II. **3**: 131. 1903. *Caraguata sintenisii* Baker, Handb. Bromel. 145. 1889, as *sintenesii* = **Vriesia sintenisii** (Baker) Sm. & Pitt. comb. nov. Petals appendaged, free—LBS.

T. spectabile Mez & Wercklé, Bull. Herb. Boiss. II. **4**: 873. 1904 = **Vriesia spectabilis** (Mez & Wercklé) Sm. & Pitt. comb. nov.

T. splitgerberi (Mez) Pittendrigh, Evolution **2**: 60. 1948. *Guzmania splitgerberi* Mez in DC. Monogr. Phan. **9**: 930. 1896 = **Vriesia splitgerberi** (Mez) Sm. & Pitt. comb. nov. Petals appendaged, connate—CSP.

T. squarrosum Mez & Sodiro, Bull. Herb. Boiss. II. **4**: 877. 1904 = **Guzmania squarrosa** (Mez & Sodiro) Sm. & Pitt. comb. nov. See L. B. Smith, Caldasia no. **5**: 7. 1942.

T. standleyi L. B. Smith, Contr. Gray Herb. **117**: 30, *pl. 2, figs. 30, 31*. 1937 = **Vriesia standleyi** (L. B. Smith) Sm. & Pitt. comb. nov. Petals appendaged—LBS.

T. stenophyllum Mez & Wercklé, Bull. Herb. Boiss. II. **4**: 875. 1904 = **Vriesia stenophylla** (Mez & Wercklé) Sm. & Pitt. comb. nov.

T. turbinatum Mez & Wercklé, Bull. Herb. Boiss. II. **4**: 1122. 1904 = **Vriesia turbinata** (Mez & Wercklé) Sm. & Pitt. comb. nov.

T. urbanianum (Mez) Mez, Bull. Herb. Boiss. II. **3**: 131. 1903. *Guzmania urbaniana* Mez in DC. Monogr. Phan. **9**: 920. 1896 = **Vriesia antillana** Sm. & Pitt. nom. nov. Not *Vriesia urbaniana* Harms, Notizblatt **12**: 532. 1935. Petals appendaged—LBS.

T. violascens Mez & Wercklé, Bull. Herb. Boiss. II. **4**: 877. 1904 = **Vriesia violascens** (Mez. & Wercklé) Sm. & Pitt. comb. nov.

T. viride Mez & Wercklé, Bull. Herb. Boiss. II. **4**: 872. 1904 = **Vriesia viridis** (Mez & Wercklé) Sm. & Pitt. comb. nov. Petals appendaged, free—LBS.

T. vittatum Mez & Wercklé, Bull. Herb. Boiss. II. **4**: 871. 1904 = **Vriesia vittata** (Mez & Wercklé) Sm. & Pitt. comb. nov.

T. werckleanum Mez, Bull. Herb. Boiss. II. **3**: 139. 1903 = **Vriesia nephrolepis** Sm. & Pitt. nom. nov. Not *Vriesia werckleana* Mez. Bull. Herb. Boiss. II. **3**: 136. 1903.

T. wittmackii André, Brom. Andr. 107, *pl. 39B*. 1889: Mez, Bull. Herb. Boiss. II. **3**: 131. 1903 = **Guzmania wittmackii** (André) André ex Mez in DC. Monogr. Phan. **9**: 921. 1896. Petals naked, agglutinated—LBS.

André based *Thecophyllum* on two species with free sepals and fascicles of flowers in the axils of large primary bracts. On the basis of a subsequent collection (*Haught* 2897), we know that the first of these, *T. wittmackii*, has the flowers of a *Guzmania*. The description of the second species, *T. poortmanii*, was based on Poortman's sketch of the plant, and as this indicated a long and exserted corolla-tube, there is little doubt that it also is a *Guzmania*.

In 1896, in his first monograph of the Bromeliaceae (DC. Monogr. Phan. **9**), Mez reduced *Thecophyllum* to a subgenus of *Guzmania*, adding 12 more species to the concept and dropping the character of free sepals.

In 1903, Mez discovered that one of these added species, *G. ororiensis*, had the flowers not of a *Guzmania* but of a *Vriesia*. Whereupon he re-

moved them all from *Guzmania* and resurrected *Thecophyllum* as a genus related to *Vriesia* but differing in its aborted branches.

From then until his second monograph (Engler, das Pflanzenreich IV. **32**), Mez added 33 more species including 15 with "ramulis manifestis." These last contradicted André's original basis and required a complicated redefinition of the genus. Although L. B. Smith had reduced the comparably artificial genus, *Sodiroa* (Contr. Gray Herb. **104:** 73), and demonstrated that several supposed species of Mez's *Thecophyllum* were in reality *Guzmania*, he continued with considerable inconsistency to follow Mez's lead in maintaining *Thecophyllum* as a genus (Pflanzenreich IV. **32:** 599–600).

In reducing Mez's concept of *Thecophyllum* to *Vriesia*, we note that so far as flowers are available, all species show the included stamens of the section *Xiphion*, and most of them have also the thick coriaceous sepals so common in this section. As it does not seem possible to separate Mez's *Thecophyllum* as a whole from the previously recognized species of section *Xiphion*, there is no point in trying to maintain it in an infrageneric category. Its merging with section *Xiphion* is logical from a geographical standpoint also, as that is the only section whose area completely surrounds it.

Cipuropsis Ule

Cipuropsis Ule, Verhandl. Bot. Ver. Brandenburg **48:** 148. 1907; Mez, Engl. Pflanzenreich IV. **32:** 598. 1935 = **Vriesia** Lindl. Bot. Reg. **29:** *pl. 10.* 1843.

C. subandina Ule, Verhandl. Bot. Ver. Brandenburg **48:** 149. 1907. *Tillandsia subandina* (Ule) Mez ex L. B. Smith, Contr. Gray Herb. **98:** 16. 1932; in Macbride, Fl. Peru, Field Mus. Pub. Bot. **13:** 556. 1936. = **Vriesia subandina** (Ule) Sm. & Pitt. comb. nov.

The genus *Cipuropsis* was erected by Ule to accept his species *subandina* which he observed had not only petal-appendages but also a gamopetalous corolla. We show above that no real justification existed for such action since *Vriesia psittacina*, the type of Lindley's genus, has the petals both appendaged and joined. Ule clearly took at face value Mez's polypetalous definition of *Vriesia*.

L. B. Smith's transfer of the species to *Tillandsia* was according to Mez's supposed distinction between petal-scales of *Vriesia* with a horizontal line of attachment and vertical calli with auricled apices found in some species formerly placed in *Tillandsia* (see Contr. U. S. Nat. Herb. **29:** 430). The character of gamopetaly was either overlooked or attributed to faulty observation. Later, in his last monograph, Mez accepted *Cipuropsis* as a distinct genus.

As Ule's specimen is not available it is not possible to decide which type of gamopetaly is involved, the primary or true fusion which would make *Cipuropsis* a synonym of *Vriesia* or the secondary or agglutination type which would cause it to replace the later *Mezobromelia*.

Two characters of *Cipuropsis* incline us to place it with *Vriesia* rather than with *Mezobromelia*, the shortness of its corolla-tube and the distichous arrangement of its flowers. In *Vriesia* the corolla-tube, when present, is much shorter than the sepals, in *Cipuropsis* it is described as little more than a fourth as long as the sepals, but in *Mezobromelia* it equals them. In *Vriesia* the flowers are two-ranked with very few exceptions and they are two-ranked in *Cipuropsis*, but not in *Mezobromelia*.

Chirripoa Suesseng.

Chirripoa Suesseng. Bot. Jahrb. **72:** 293, *pl. 4, fig. 11*, 1942 = **Guzmania** R. & P. Fl. Per. **3:** 37. 1802.

C. solitaria Suesseng. Bot. Jahrb. **72:** 293, *pl. 4, fig. 11*, 1942 = **Guzmania polycephala** Mez & Werckle, Repert. Sp. Nov. Fedde **14:** 254. 1916; L. B. Smith in Woodson, Fl. Panama, Ann. Mo. Bot. Gard. **31:** 116. 1944.

The genus *Chirripoa* is a prime example of the confusion involved in making genera on habital characters, since the author in noting its affinities, compared it to genera in all three subfamilies of the Bromeliaceae. In fact he was so much in doubt that he published it as "nov. genus ad interim" indicating that the name was merely a means of noting the species until its genus could be discovered.

We find that the description and plate of *Chirripoa solitaria* agree closely with *Guzmania polycephala* with one exception. The description gives a greater length for the sepals than for the floral bracts. However, the illustration does not show exserted sepals and we can only suppose that through some error only the exposed apex of the floral bract was measured, disregarding the base covered by the bract below.